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SPECIAL ISSUE: NEXT GENERATION BIOLOGICAL CONTROL

Next generation biological control – an introduction

Sophie Le Hesran[1,2], Erica Ras[3], Eric Wajnberg[4,5] & Leo W. Beukeboom[6]*

[1]*Koppert BV, Veilingweg 14, PO Box 155, 2650 AD Berkel en Rodenrijs, The Netherlands,* [2]*Laboratory of Entomology, Wageningen University, PO Box 16, 6700 AA Wageningen, The Netherlands,* [3]*Löwengasse 1B-10, 1030, Wien, Austria,* [4]*INRA, 400 Route des Chappes, BP 167, 06903 Sophia Antipolis Cedex, France,* [5]*INRIA, Sophia Antipolis, Projet Hephaistos, 2004 Route des Lucioles, BP 93, 06902 Sophia Antipolis Cedex, France, and* [6]*Groningen Institute for Evolutionary Life Sciences, University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands*

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In the past decades, human population growth has been the source of two major concerns: providing sufficient food for humanity and minimizing worldwide environmental pollution (DeBach & Rosen, 1991). Crop production can be reduced substantially by abiotic and biotic stressors, like shortage or excess of water, extreme temperatures, low nutrient supply, weeds, pathogens, and pests (Oerke, 2006). Although chemical pest control has been essential in achieving great increases in crop yields, the massive overuse and frequent misuse of chemical pesticides has resulted in serious environmental and human health problems, and in the emergence of insects and mites resistant to these pesticides. In a similar way, genetic modification of crops to build pest and herbicides resistance resulted in many concerns, such as an indirect increase in the use of herbicides, the development of pest resistance, and even negative effects on human health (Magaña-Gómez & Calderón de la Barca, 2017; Woodbury et al., 2017). The most successful alternative to chemical pest control and the use of genetically modified crops is biological control by natural enemies (Heimpel & Mills, 2017). It can be defined as the use of living organisms (called natural enemies) to suppress the population density or impact of a specific pest organism, making it less abundant or less damaging than it would otherwise be (Eilenberg et al., 2001).

Biological control includes the control of invertebrate pests using predators, parasitoids and pathogens, the control of weeds using herbivores and pathogens, and the control of plant pathogens using antagonistic micro-organisms and induced plant resistance (Eilenberg et al., 2001). These natural enemies can be used in three major ways: (1) importation of exotic species and their establishment in a new habitat (also called classical biological control); (2) augmentation of established species by mass production and periodic colonization (augmentative biological control); and (3) their conservation through manipulation of the environment (conservation biological control) (DeBach & Rosen, 1991). While the species used in classical biological control are exotic for the habitat in which they are introduced, those used in augmentative biological control may be indigenous or exotic (van Lenteren, 2012).

Classical biological control has been successful in many cases: one of the most famous examples dates back to 1889, when the Australian vedalia lady beetle, *Rodolia cardinalis* (Mulsant), was introduced into California (USA) orange groves by Charles Valentine Riley, and successfully controlled the cottony cushion scale, *Icerya purchasi* Maskell (Howarth, 1991). Augmentative biological control is an effective, environmentally and economically sound alternative for chemical pest control, and its use has increased since the development of biocontrol companies in the last decades. However, in both classical and augmentative biological control, the introduction of exotic species in a new environment can also have negative impacts: although examples are scarce, they can attack non-target organisms, sometimes leading to species extinctions; they can disrupt established populations, sometimes enhancing the targeted pest; and they can affect public health (Howarth, 1991). Therefore, an increasing number of guidelines and regulations, such as the 'Guidelines for the export, shipment, import and release of biological control agents and other beneficial organisms' (IPPC, 2005) have been implemented over the years to prevent such negative impacts. In addition, the collection of exotic

*Correspondence: Leo W. Beukeboom, Groningen Institute for Evolutionary Life Sciences, University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands. E-mail: l.w.beukeboom@rug.nl

species in foreign countries is becoming more and more regulated. Under the Convention on Biological Diversity (CBD, 1992), countries have sovereign rights over their genetic resources. Access to these resources and sharing of the benefits arising from their use has to be agreed between involved parties, especially since the adoption of the Nagoya Protocol on Access and Benefit Sharing in 2010 (Cock et al., 2010; van Lenteren, 2012). Recent applications of CBD principles have already made it difficult or impossible to collect and export natural enemies for biocontrol research in several countries (Cock et al., 2010). For all these reasons, there has been a recent trend to first look for indigenous natural enemies in augmentative biological control (van Lenteren, 2012).

Nowadays, likely over 230 species of natural enemies are commercially available and used in augmentative biological control (van Lenteren, 2012). Ensuring the efficacy of these natural enemies is not always simple, as their performance as biocontrol agents can be affected by many abiotic and biotic factors, such as unfavorable climatic conditions, the presence of chemical pesticides, potential attack by predators, the existence of plant defense mechanisms, and potential deleterious effects of unwanted breeding selection and inbreeding in mass-rearing programs. In addition to looking for new indigenous natural enemies, the possibility to 'improve' the efficacy of a potential biocontrol agent has also attracted the attention of researchers and biocontrol companies over the last century (Mally, 1916; DeBach, 1958; Roush & Hoy, 1981; Hoy, 1986, 1990; Rosenheim & Hoy, 1988; Wajnberg, 2004; Seko & Miura, 2009; Lommen et al., 2017; Kruitwagen et al., 2018). However, as already mentioned several times, there is still much to learn on the improvement of natural enemies and augmentative biological control, and many challenges are still ahead, including: (1) a better understanding of the genetic processes related to adaptation and selection of natural enemies; (2) choosing the right traits to select for in terms of biocontrol efficacy and understanding the genetic basis of these traits; (3) evaluating the existing genetic variation for these traits within and among populations; (4) choosing an adequate method of selection; and (5) maintaining the selected traits in mass-reared populations before an improved biocontrol agent can be released. This special issue addresses many aspects of these challenges in applying genetic and genomic knowledge to improve biocontrol agents, a development that is being referred to as 'next generation biocontrol'. The publications are based on papers presented at the First International Conference of Biological Control (Beijing, China, May 2018) or at the European Conference of Entomology (Naples, Italy, July 2018), the latter by members of the Marie Skłodowska-Curie Innovative Training Network on Breeding Insects for Next Generation Biological Control (BINGO, 2014-2019).

This issue contains two reviews of the influence of rapid evolution on biocontrol agents: how this can be used in a breeding setting (Lirakis & Magalhaes, 2019) and how natural selection can improve the biocontrol agent in the field (Szücs et al., 2019). Lirakis & Magalhaes (2019) comprehensively review the literature on the use of experimental evolution and artificial selection to improve native biocontrol agents. The authors critically evaluate the methodologies used and provide recommendations for future studies. They conclude that, if applied correctly and combined with new genomic methods, experimental evolution and artificial selection can be powerful and promising tools to improve the biocontrol efficacy of natural enemies. Complementarily, Szücs et al. (2019) focus on the strong natural selection imposed on populations of natural enemies introduced in a new environment, and its potential consequences on population growth, life-history traits, and biocontrol efficacy. The authors review modeling, laboratory, and field studies, and show that the potential changes in a biocontrol agent following its introduction in a new environment are likely to be larger than previously considered. An example of such changes is then provided by the study of Griffith et al. (2019), in which it is demonstrated that the weed biocontrol agent *Eccritotarsus catarinensis* (Carvalho) (Hemiptera: Miridae) underwent post-release adaptation to environments with temperatures beyond those in its native range. Such change in temperature tolerance is likely to be caused by a combination of phenotypic plasticity and rapid evolution. The authors conclude that biological control practitioners could take advantage of the thermal plasticity of biocontrol agents and the micro-evolutionary changes that might occur post-release in order to maximize the impact of biocontrol agents across a broad range of thermal environments.

Genetic variation is crucial in wild populations of biocontrol agents to ensure their survival under fluctuating environmental conditions and in diverse ecosystems. Three studies in this issue focus on the effects of genetic variation within and among populations on biocontrol efficacy, and on its use to improve the efficacy of biocontrol agents. Artificial selection for insecticide resistance in a natural enemy, a controversial topic in biological control, is investigated by Balanza et al. (2019). They show that variation in tolerance to neonicotinoid insecticides among populations of the biocontrol agent *Orius laevigatus* (Fieber) (Hemiptera: Anthocoridae) can be exploited to optimize its performance in the field. However, the authors stress that selection for insecticide resistance may have negative effects on fitness components of the selected strains, and that further studies are needed before resistant *O. laevigatus* can be used in biocontrol programs. Lommen et al. (2019) performed artificial selection on wing truncation in the biocontrol agent *Adalia bipunctata* (L.) (Coleoptera: Coccinellidae) to ensure that it remains close to its place of release. They found that genetic variation for the extent of wing truncation in *A. bipunctata* is cryptic: this genetic variation does not seem to contribute to the phenotype variation observed under standard conditions experienced by natural populations, but only leads to the wingless phenotype under specific temperatures. The extent of wing truncation has a high heritability in the population studied, albeit depending on temperature. These results provide information on the genetic basis of wing truncation in *A. bipunctata* and reveal potential for improving this biocontrol agent. Bestete et al. (2019) report the appearance of a yellow variant of the Neotropical green lacewing *Chrysoperla externa* (Hagen) (Neuroptera: Chrysopidae) in their laboratory culture. This color difference among individuals could have a genetic basis or be due to phenotypic plasticity exhibited in response to changing environmental conditions. The difference in body pigmentation was hypothesized to have an effect on life-history traits, like behavior, immune responses, and more generally on the performance of this biocontrol agent. The authors found a simple genetic basis for this alternative form and no difference in performance in terms of life-history traits between the yellow and the green individuals.

The importance of genetic variation in commercial populations of insects has long been realized, and unwanted selection under rearing conditions, along with inbreeding, may severely decrease the efficacy of natural enemies upon release (Stouthamer et al., 1992; Wajnberg, 2004; Zayed & Packer, 2005). Leung et al. (2019) studied the potential effects of inbreeding and polyploidy in the parasitoid wasp *Nasonia vitripennis* (Walker) (Hymenoptera: Pteromalidae). They emphasize that results on this model species can be used to judge the possible pros and cons of using polyploids in biological control programs. Additionally, Paspati et al. (2019) investigate the effects of long-term mass rearing on the genetic diversity of the predatory mite *Amblyseius swirskii* Athias-Henriot (Acari: Phytoseiidae) by analyzing microsatellite markers. They investigated a commercially reared *A. swirskii* population and found a 2.5-fold reduced heterozygosity compared to its wild counterparts, which may reduce its performance to control pests upon release. The authors stress the importance of performing additional genetic analysis of more commercial populations to further assess the impact of genetic diversity on the performance of *A. swirskii* as a biocontrol agent. For this, they recommend to use a pooled microsatellite analysis, a cost-effective method to determine the genetic diversity of minute biocontrol agents.

Molecular tools like microsatellite markers can help in determining the genetic diversity in biocontrol agent populations, but also in distinguishing between species and strains of biocontrol agents. Paterson et al. (2019) compared host-specificity and efficacy of two cryptic species of a water hyacinth biocontrol agent in South Africa, *E. catarinensis* and *Eccritotarsus eichhorniae* Henry (Hemiptera: Miridae). The species originate from Brazil and Peru, do not interbreed, and can be distinguished based upon the cytochrome oxidase I (COI) sequence of their mitochondrial DNA. The authors found significant differences in performance between the two species, depending on temperature. They highlight the importance of distinguishing populations of biocontrol agents from different native ranges, as there is a risk that cryptic species may be inadvertently released with consequences on biocontrol efficacy. Finally, Stahl et al. (2019) report an example of the use of molecular tools to improve biological control. They developed a genetic test to screen for the presence of *Anastatus bifasciatus* Geoffroy (Hymenoptera: Eupelmidae) in field-collected samples of their hosts, the eggs of the agricultural pest *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae). This molecular tool can be used both in field and laboratory studies to better interpret host-parasitoid and parasitoid-parasitoid interactions. It can also be useful for risk assessment to test whether the biocontrol agent can unwantedly target other species.

Overall, this special issue provides insight into the use of natural genetic diversity, artificial selection, and molecular tools to potentially improve biocontrol efficacy. We hope it will convince readers that biological control can benefit greatly from these approaches, in combination with the exploration for new indigenous natural enemies. The concepts of biological control and selective breeding are explained in two – free to use – videos, entitled 'Biological control in agriculture – The invisible world of mites' (https://www.youtube.com/watch?v=LDml80dENo0&feature=youtu.be) and 'Biological control in agriculture – Selective breeding' (https://www.youtube.com/watch?v=3kGla8YQvV0&feature=youtu.be). Scientists have an important role in the promotion of biological control to the general public, and we think that videos like these may be a relevant medium for communication on this important topic.

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